Animal Conservation (2003) **6**, 207–219 © 2003 The Zoological Society of London
DOI:10.1017/S1367943003003263 Printed in the United Kingdom

Altered behaviour in spotted hyenas associated with increased human activity

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(Received 17 June 2002; accepted 5 December 2002)

Abstract

To investigate how anthropogenic activity might affect large carnivores, we studied the behaviour of spotted hyenas (*Crocuta crocuta*) during two time periods. From 1996 to 1998, we documented the ecological correlates of space utilization patterns exhibited by adult female hyenas defending a territory at the edge of a wildlife reserve in Kenya. Hyenas preferred areas near dense vegetation but appeared to avoid areas containing the greatest abundance of prey, perhaps because these were also the areas of most intensive livestock grazing. We then compared hyena behaviour observed in 1996–98 with that observed several years earlier and found many differences. Female hyenas in 1996–98 were found farther from dens, but closer to dense vegetation and to the edges of their territory, than in 1988–90. Recent females also had larger home ranges, travelled farther between consecutive sightings, and were more nocturnal than in 1988–90. Finally, hyenas occurred in smaller groups in 1996–98 than in 1988–90. We also found several changes in hyena demography between periods. We next attempted to explain differences observed between time periods by testing predictions of hypotheses invoking prey abundance, climate, interactions with lions, tourism and livestock grazing. Our data were consistent with the hypothesis that increased reliance on the reserve for livestock grazing was responsible for observed changes. That behavioural changes were not associated with decreased hyena population density suggests the behavioural plasticity typical of this species may protect it from extinction.

INTRODUCTION

Although increasing human population density is often associated with decline or extinction of local carnivore populations (Woodroffe & Ginsberg, 1998; Woodroffe & Ginsberg, 1998, 2000), few studies have examined how human activity directly affects large carnivores (Frank & Woodroffe, 2001; Sunquist & Sunquist, 2001). The literature on basic ecology of mammalian carnivores (e.g. Gittleman & Harvey, 1982) suggests that, if growing human populations negatively affect habitat quality for carnivores, then increasing human activity should be associated with increased home-range size and energy expenditure, and with decreased carnivore population density. However, because some predators are more sensitive than others to anthropogenic activity (Woodroffe, 2000; Sunquist & Sunquist, 2001), effects of habitat degradation may vary considerably among species. Species exhibiting greater behavioural plasticity are expected to be able to adapt more readily than others to life in proximity to humans (Woodroffe, 2000). Here we focus on behavioural changes associated with increasing human population density observed during a long-term study of one large social group, or clan, of spotted hyenas (*Crocuta crocuta*) inhabiting a territory at the edge of a wildlife reserve in East Africa (Fig.1(a)). *Crocuta* are extremely flexible in their behaviour and ecology. They breed throughout the year, they may be either diurnal or nocturnal, they occupy a vast array of habitat types, and they eat carrion as well as live prey ranging in size from termites to elephants (Kruuk, 1972; Cooper, 1990*b*; Mills, 1990; Sillero-Zubiri & Gottelli, 1992; Holekamp *et al.*, 1997*b*; Hofer & Mills, 1998; Holekamp *et al.*, 1999). Thus their responses to long-term environmental changes should represent conservative indicators of how top predators in general may respond to such changes (Arcese & Sinclair, 1997), and their behavioural plasticity may protect them from extinction.

Between 1996 and 1998, we investigated possible ecological determinants of the space utilization patterns exhibited by adult female hyenas, including distributions of ungulate prey, vegetative cover, lions (*Panthera leo*), tourism and livestock grazing. We found that hyenas were

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seldom observed in that portion of their group territory in which prey animals were most abundant (Boydston, 2001). This surprising observation suggested that our study animals might be incurring unusually heavy energetic costs, either by commuting from surrounding habitat to the area of greatest prey abundance or by foraging in areas containing lower prey densities. We therefore used archived data to compare space utilization by hyenas in 1996–98 with that by hyenas of comparable social ranks in 1988–90, when human population density adjacent to the hyenas' territory was still relatively low. Finding that patterns of space utilization differed significantly between the two time periods, we inquired whether social behaviour and temporal activity patterns differed as well. We also tested predictions of hypotheses suggesting causal explanations for the observed behavioural changes between the two time periods. Specifically, we investigated correlated changes in climate, prey abundance, rates of hyena interaction with lions, tourism and pastoralist activity. Our final goal was to determine whether demographic changes had occurred between the two time periods in association with observed behavioural changes.

METHODS

Study animals and study site

A *Crocuta* clan contains multiple adult females, their offspring, and one to several adult immigrant males. Females give birth to litters of one or two cubs (Kruuk, 1972; Mills, 1990; Holekamp, Smale & Szykman, 1996) that are reared at dens for the first 8–10 months of life. Females are generally philopatric, but most males disperse (Frank, 1986*b*; Henschel & Skinner, 1987; Smale, Nunes & Holekamp, 1997; Holekamp & Smale, 1998*a*; East & Hofer, 2001). Social relationships within a clan are organized on the basis of a linear dominance hierarchy, and an individual's position in this hierarchy determines its priority of access to food (Tilson & Hamilton, 1984; Frank, 1986*b*; Mills, 1990). Clans are fission–fusion societies in which individuals are most often found in small subgroups (Holekamp *et al.*, 1997*a*). Our study clan, which usually contains 60–80 hyenas, defends a territory of 62 km^2 (Boydston, Morelli & Holekamp, 2001) in the Talek region of the Masai Mara National Reserve (henceforth, the Reserve; Fig.1(a)). This is an area of open rolling grassland grazed year-round by large concentrations of resident ungulates which are joined for 3 or 4 months each year by large migratory herds. Spotted hyenas are opportunistic hunters, targeting whichever prey species are locally most abundant (Kruuk, 1972; Cooper, 1990*b*; Holekamp *et al.*, 1997*b*).

Between 25 May 1988 and 31 December 2000, observers monitored Talek hyenas for approximately 6 hours per day on 4106 days. Most behavioural data were collected between 05.30 and 09.00 hours, and between 17.00 and 20.00 hours, supplemented with observations made at midday, and at night using night-vision binoculars. Each hyena was identified by its unique spots, and sexed on the basis of penile morphology (Frank, Glickman & Powch, 1990), and its age was known to within ± 7 days (Holekamp & Smale, 1993; Holekamp *et al.*, 1996). Adult females were those over 3 years of age and younger females that had already conceived their first litters. Males were considered to be adults at 2 years of age. Females younger than 3 years who had not yet conceived their first litters, and males younger than 2 years, were considered to be juveniles. All hyenas born in Talek were considered to be resident animals, as were those adult males who had emigrated from other clans but had been present in Talek for at least 6 months.

From 1988 to 2000, we searched daily for hyenas by driving throughout the Talek area and stopping to scan with binoculars from all high points. Each time we found one or more hyenas separated from other hyenas by at least 200 m, an observation session was initiated. The session ended when observers left that individual or group. The location of each observation session was recorded in reference to local landmarks, or as geographic coordinates using a Global Positioning System (GPS). Date, time, number of hyenas present, and presence or absence of lions with the hyenas were also recorded for every observation session.

Spatial data

Study site maps

A digital base map of the Talek territory and surrounding habitat was created from 1:20,000 air photos taken in 1991 by Kenya Wildlife Service and Kenya Rangelands and Ecological Monitoring Unit, as described in Boydston *et al.* (2003). As separate coverages, the boundaries of the clan's territory and locations of all dens used by Talek hyenas during the study were digitized (Fig. 1(a)).

Vegetation map

A vegetative cover map with 50 m resolution was digitized from the 1991 air photos. Each grid cell was assigned to one of three vegetative classes: 'grass' cells contained short or long grass with less than 10% of their area covered by bushes or trees; 'moderate cover' cells contained 10–50% bushes or trees; 'dense cover' cells contained more than 50% bushes or trees.

Lion locations

In 1996–98, all locations at which lions were sighted were recorded and digitized as a GIS layer. In addition to recording all locations of lions observed with hyenas, we also regularly found lions by investigating all clusters of tour vehicles. Each sighting of a lion or a group of lions was counted as a single location. A utilization distribution (UD) grid showing the areas of highest probability of lion use was then calculated with the Animal Movement Extension (Hooge & Eichenlaub, 1997).

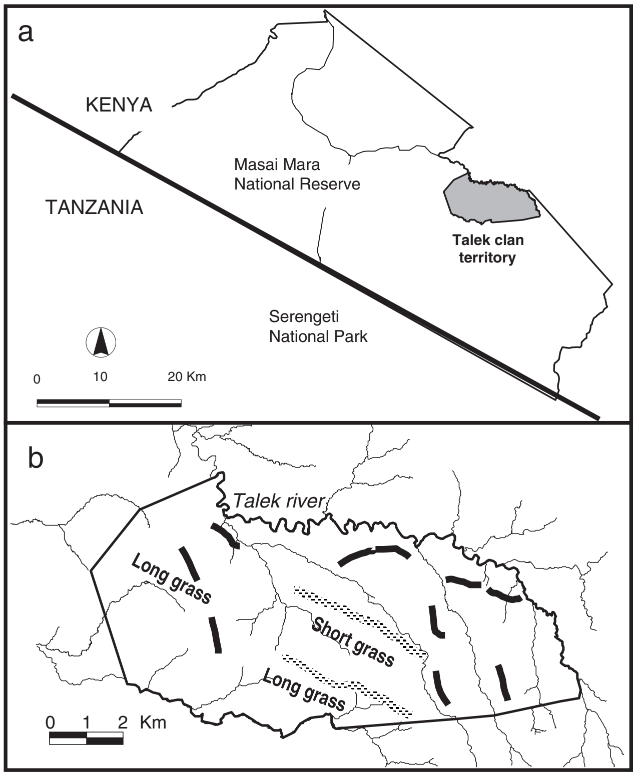

Fig. 1 (a) Map of the Talek clan territory (shaded in gray) in relation to the boundary of the Masai Mara National Reserve. (b) Transects used to estimate numbers of ungulates once per week during 1996–98. The two transects shown as stippled lines were also run in 1988–90, once every 2 weeks. Each of these original transects was 4 km long, one in short-grass habitat and one in long grass. The main areas of long grass and short grass inside the territory are labelled. The unlabelled area to the east was heterogeneous habitat of grass, bush and acacia woodland.

Ungulate prey

Prey available to Talek hyenas were monitored by weekly counts of all native ungulates found within 100 m of 18 km of transect lines (Fig. 1(b)). Prey counts were averaged bi-weekly, and raster maps (500 resolution) of relative ungulate abundance for each prey census date were created using ArcView with Spatial Analyst. To derive these raster maps, each 1 km transect was digitized as three points, and for each transect day, each point was assigned the attribute of one-third the total number of ungulates counted on that 1 km transect. A 'surface' of prey densities was then interpolated with an inverse-density-weight function. Maps for multiple dates were integrated to examine spatial distributions of prey over longer time intervals.

Tourism

From September 1996 to March 1998, numbers of tour vehicles in the Talek clan's territory were counted during 30 minute sampling periods conducted between 07.30 and 09.00 or 16.30 and 18.00. These vehicle counts were conducted up to three times per week and averaged for each bi-weekly interval. We then compared hyena space utilization during a period of relatively low and a period of relatively high numbers of vehicles.

Livestock and pastoralists

GPS locations of pastoralist settlements were recorded in a field survey in 2000 and digitized as a GIS layer. Each discrete village or fenced livestock enclosure was digitized as a single point. Livestock were typically corralled every evening inside villages or fenced enclosures, and herded out to surrounding grazing areas each morning, accompanied by armed herders.

We used two methods in 1996–98 to identify areas within the Talek clan's territory that pastoralists utilized for grazing livestock, and to document numbers of livestock present. First we ran a transect along the south side of the Talek river to provide a conservative estimate of total livestock numbers inside the territory. This transect was run up to three times weekly between 08.30 and 10.00 and between 16.30 and 18.00, the times of day when herds were most likely to be entering or leaving the Reserve, respectively. Herds within 2 km of the Talek river could be seen from the transect line, and location, size and type (cows, goats or sheep) were recorded for each herd seen. Second, in May 1997, we began conducting weekly livestock surveys near midday, by which time herds had travelled their maximum distances into the Reserve. Each survey involved driving a circuit through the entire Talek territory and scanning from high points to locate all livestock herds. Raster maps representing the relative extent to which pastoralists utilized different areas (500 resolution) for grazing domestic livestock were created through surface interpolation using ArcView with Spatial Analyst. In the GIS, a 'surface' of relative grazing intensity was interpolated from the data for each survey date, incorporating both locations and sizes of herds.

Hyena locations

Between July 1996 and April 1998, we documented space utilization patterns of 13 adult female *Crocuta*, spanning social ranks from rank 2 (highest) to 26 (lowest). The females were fitted with radio-collars (Telonics Inc., Mesa, AZ) transmitting in the 150–151 MHz range, and were tracked daily from vehicles equipped with scanning receivers. Locations of each tagged hyena were pinpointed by either sighting it or localizing its signal to an area less than 200 m^2 when the hyena was not visible.

Each week, we attempted to acquire at least three radio-tracked locations per female. The clan's entire territory was driven at least once every 2 days, and special efforts were made both inside and outside the territorial boundaries to track any collared females not found during the preceding few days. As we drove our regular circuits, we also recorded locations of radio-collared females found without use of telemetry equipment. Each time a female was found, her geographic location was recorded in reference to local landmarks or as the mean of 3–5 readings on a hand-held Magellan GPS that was accurate to ± 100 m. Date and time were also recorded. Locations for each female were separated by at least 1 hour. One hour allowed sufficient time for hyenas to cross the Talek territory, and was thus sufficient for statistical independence of observations (White & Garrott, 1990). All locations within 200 m of the communal den were excluded to avoid biasing spatial data towards den sites, which observers usually visited at least twice daily.

All locations were digitized and associated with UTM coordinates. To document space utilization patterns, we calculated linear distances and home-range estimates for each hyena using ArcView software with the Animal Movement Extension (Hooge & Eichenlaub, 1997). For each location for each female, we obtained the straight-line distance from that point to the current communal den within the Talek territory, and also the distance between that point and the nearest territorial boundary or 'edge' (Boydston *et al*., 2003). The distance to the nearest territorial boundary ('distance to edge') was used as a measure of a female's tendency to be peripherally located. If a female was found outside the Talek territory, her distance to the nearest boundary was assigned a negative value. Home-range sizes were estimated using fixed kernel utilization distributions (UDs: Worton, 1989; Powell, 2000) with 95% probabilities for all females individually (e.g. Boydston *et al*., 2003) and collectively (e.g., Fig. 2(a–b)). UDs were transformed to a log scale for statistical analysis.

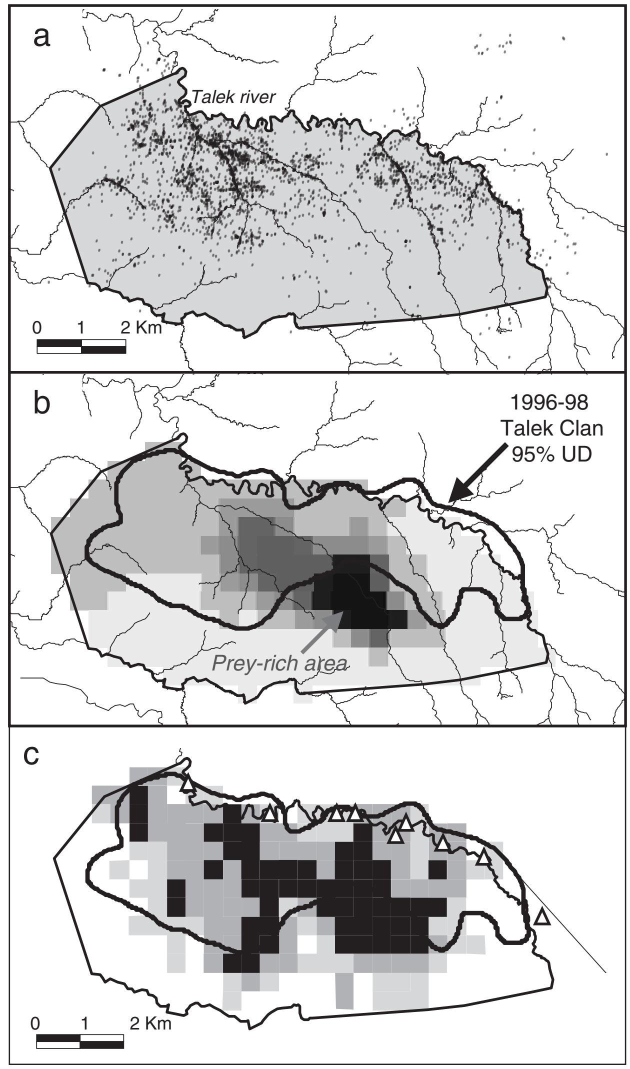

Fig. 2 (a) All locations (*n* = 4838, including both tracked and non-tracked locations) at which 13 Talek female hyenas were found in 1996–98. (b) The collective 95% UD contour created from the points depicted in (a), shown in relation to a grid indicating prey abundance. Grid cells in shades of gray represent relative levels of ungulate prey abundance, with the darkest cells containing the most abundant wild ungulates at any given time. Prey census data are depicted here in 500 resolution for ease of comparison with Fig 2(c). (c) Grid cells showing relative intensity of use by cattle and pastoralists, with the darkest cells containing the most abundant livestock at any given time. River crossings used by cattle are indicated by triangles.

Historical comparison of 1988–90 with 1996–98

Hyena locations

Locations at which Talek females were found in 1996–98 were compared to those from 1988–90, which was the earliest period for which such data were available. This earlier period was typical of conditions recorded in Talek since 1979 (Frank, 1986*a*). The temporal patterning of our observations and our methods for finding hyenas in both periods were identical with three exceptions. First, no adult female hyenas wore radio collars in 1988–90, so only locations of females found without telemetry were used in historical comparisons. Second, in contrast to 1996–98, we made no systematic attempts in 1988–90 to search for females outside the Talek territory boundaries when they were not found for 2–3 days. In both periods we excluded locations of females found at dens and locations not separated by at least 1 hour for each female. Third, circuits throughout the Talek area were usually driven by one vehicle in 1988–90 and by two vehicles in 1996–98.

Locations for 13 Talek females observed between September 1988 and April 1990 were digitized from archived field notes and compared to those from September 1996 to April 1998. Females studied in 1988–90 were matched by social rank with females monitored in 1996–98. We compared mean values for the 13 females monitored during each time period with respect to UD size, distance to the den, distance to the nearest territory boundary, distance between consecutive sightings of the same animal corrected for time elapsed, and distance at which hyenas were found from the nearest grid cell containing dense vegetative cover. We also compared mean group size between 1988–90 and 1996–98 by comparing between periods the mean number of hyenas present per session, over all hours of the day. Only sessions in which hyenas were found without telemetry were used in this analysis.

Meteorological data

Rainfall measurements were recorded daily throughout both time periods at one location within the Talek territory. Mean daily temperatures each month were also available for both periods from Jomo Kenyatta Airport, Nairobi, located 170 km northeast of Talek.

Rates of lion–hyena interaction

The rate at which Talek hyenas encountered lions within their territorial boundaries was calculated for each month during each time period as: number of sessions in which lions and hyenas were present together/total number sessions in which Talek hyenas were observed. Monthly mean rates were then compared between the two time periods.

Ungulate prey

Prey abundance during both time periods was monitored by counting all ungulates found within 100 m of transect lines as described above. Two ungulate census transects of 4 km each, one in short grass and one in long grass, were run at bi-weekly intervals in both 1988–90 and 1996–98 (indicated by stippled lines in Fig. 1(b)), and mean count values from these two transects were directly compared between periods.

Tourism

We did not collect systematic data on numbers of tour vehicles observed in Talek in 1988–90, as we did in 1996–98. However, we refer to work by other researchers for trends in tourism and numbers of tourists visiting the Reserve (Gakahu, 1992; Bhandari, 1999; Walpole *et al*., 2003).

Settlements and livestock

To represent locations of pastoralist settlements in 1988–90, settlements were digitized from 1991 air photos. The 2000 field survey data were assumed to offer an accurate representation of settlement locations in 1996–98. These data may have slightly overestimated the numbers of villages actually present during both time periods. Livestock transects were not run in 1988–90, so no quantitative comparisons of grazing pressure were possible.

Temporal aspects of hyena activity patterns

To inquire whether the temporal activity patterns of Talek hyenas shifted between periods, we compared numbers of hyenas present per observation session during our primary crepuscular viewing periods each day in 1988–89 and 1996–97. Since *Crocuta* are rarely abroad during daylight hours in the Reserve, we reasoned that failure to see hyenas known to be present in the clan during their crepuscular periods of major activity would suggest their activity had shifted from crepuscular to nocturnal, assuming clan size was no smaller in 1996–98 than in 1988–90.

Demography

To determine whether the Talek clan had undergone demographic changes between 1988–90 and 1996–98, we measured eight demographic variables on a monthly basis for the two 20-month time periods: September 1988 to April 1990 and September 1996 to April 1998. An individual hyena was counted as present in the clan during any month in which it was observed inside the Talek territory. We used five variables to examine clan size and composition: number of adults present, number of adult females present, number of juveniles present, overall clan size, and adult sex ratio (resident immigrant males:adult females). The first three of these were expressed as percentages of overall clan size. Additionally, per capita monthly mortality rates were calculated separately for adult females and juveniles, as was the average birth rate per female. Clan size was the total number of hyenas present in the clan during a given month, including all adults and juveniles. Mortality rates were calculated as the number of individuals dying during a given month divided by the number of individuals of that type alive at the beginning of that month. Male *Crocuta* less than 2 years of age have not been observed to disperse from this population (Holekamp & Smale, 1998*b*), and females rarely disperse (Frank, Holecamp & Smale, 1995), so disappearance from the clan by any individual younger than 2 years was attributed to death. Birth rate was calculated as the number of cubs born in the clan during a given month divided by the number of adult females present in the clan at the start of that month.

Statistical analyses

SYSTAT v. 8.0 was used for all statistical analyses. Sample sizes in all spatial analyses were numbers of adult females monitored. In historical comparisons, Student's *t*-tests were used to evaluate mean differences between 1988–90 and 1996–98 with respect to space-utilization measures, meteorological data, rates at which hyenas were observed interacting with lions, prey abundance, group size, numbers of tourists visiting the Reserve each year, and numbers of hyenas observed during morning and evening observation sessions. In demographic comparisons between the two time periods, we used Mann–Whitney *U*-tests (two-tailed) to evaluate differences between monthly means for each 20-month period with Bonferroni adjustment to correct for multiple tests ($k = 8$, $\alpha = 0.05$) (Rice, 1989). Means were presented with standard errors, and differences between groups were considered significant when $P < 0.05$.

RESULTS

Space utilization patterns in 1996–98 and their ecological correlates

We used 4838 hyena locations in our analyses, including a mean of 372 ± 42 locations for each of the 13 females monitored in 1996–98. On average, 66 ± 3% of these locations were obtained using telemetry equipment for each female. Talek females were found throughout the clan's territory, but some areas were far more heavily utilized than others (Fig. 2(a)). The collective 95% UD contour (Fig. 2(b)), averaged from the space utilization patterns of all 13 females, showed that hyenas intensively used the western and eastern portions of the northern half of the territory but relatively rarely utilized the central and southern regions.

Vegetation

Although most of the space defended by Talek hyenas contained open grassland, hyenas were found disproportionately often in close proximity to patches of dense vegetative cover. For example, although only 38.2% of the grid cells in the territory occurred less than 200 m from stands of dense vegetation, 68.1% of tracked hyena locations were less than 200 m from dense vegetation ($\chi^2 = 18.06$; d.f. = 1; $P < 0.001$). Thus Talek hyenas preferred to remain in proximity to dense cover, even though relatively little cover was available.

Lions

On average, 14.2 ± 1.5 individual lions or groups of lions were seen per month in the Talek home range, with an average group size of 3.7 ± 0.2 lions per sighting. Because lions represent one of the major mortality sources for spotted hyenas (Kruuk, 1972), we anticipated that hyenas might attempt to avoid areas in which lions were found. However, hyenas and lions had positively correlated spatial distributions; hyenas were more likely to be found in grid cells with higher probability of use by lions ($R_p = 0.46$, $P < 0.001$).

Ungulate prey

Prey was unevenly distributed across the Talek clan's territory (Fig. 2(b)). At any given time, much of the prey was concentrated on the short grass plains in the centre of the territory. In fact, the black grid cells in Fig. 2(b) contained almost 25% of the total prey estimated to occur in the entire territory. Comparing the collective Talek UD to the distribution of prey suggested that hyenas might be avoiding the area of their territory in which prey was most abundant (Fig. 2(b)). Of the 4789 hyena locations within the clan's territorial boundaries, only 64 (1.3%) locations fell within the area comprised of black grid squares in Fig. 2(b). Thus Talek hyenas were found in these prey-rich areas significantly less often than expected by chance ($\chi^2 = 33.80$, d.f. = 1, $P < 0.001$).

Tourism

During September to November 1996, numbers of tour vehicles ranged from four to 65 per count, while for these same months in 1997, vehicle counts ranged from one to ten. Mean numbers of vehicles counted were significantly lower in 1997 than in 1996 for these six bi-weekly intervals ($T = 2.813$, $P = 0.037$, d.f. = 5). We compared space utilization patterns for radio-collared females between these two time periods, taking advantage of the variation in tourist numbers during these months between years to control for seasonal ecological changes. On average, females were found 2.3 ± 0.9 km from the communal den when vehicle numbers were high, while female distance from the communal den was significantly higher, averaging 3.9 ± 1.5 km, when vehicle numbers were low (Paired T-test: $T = 3.523$, $P = 0.007$, d.f. = 9). Mean distance to the edge of the territory did not differ significantly between periods (Paired T-test: $T = 1.567$, $P = 0.152$, d.f. = 9).

Settlements and livestock

Throughout the 1996–98 study period, pastoralists brought livestock into the Reserve almost daily via a few specific crossing sites along the Talek river (indicated by white triangles in Fig. 2(c)). Goats and sheep usually stayed close to the Talek river, but cattle regularly grazed up to several kilometres into the Reserve from their points of entry. Cattle were grazed in the Reserve on 90% of days when observers were present in the study area. The main reason for herds not entering the park on 10% of days appeared to be high water level in the Talek river, which prevented cattle from crossing. Including days when no livestock entered the Reserve, an estimated daily average of 1580 ± 140 cows, goats and sheep were grazed each day in the Talek clan's territory. Livestock numbers exceeded 3000 on at least 20% of days, and ranged up to 6000 animals per day. Cattle were grazed throughout the Talek clan's 95% UD, but the largest area of regular and highest cattle grazing was not a part of this 95% UD. Thus hyenas were seldom found in the largest area of intensive cattle grazing (Fig. 2(c)).

Historical comparison of 1988–90 with 1996–98

Hyena space-utilization

We plotted 959 non-tracked locations for 13 Talek females in 1988–90, including a mean of 74 ± 8 locations for each of the 13 females monitored during this early period. We compared these with 1561 non-tracked locations in 1996–98, including a mean of 120 ± 16 non-tracked locations for each of the 13 females monitored during this period. The mean time elapsed between consecutive sightings of each individual female in 1988–90 was 208 ± 38 h, and was 112 ± 18 h in 1996–98. Patterns of space utilization exhibited by Talek hyenas changed dramatically between 1988–90 and 1996–98 (Fig. 3). The most striking difference between periods occurred with respect to use of the central short-grass plains: Talek females were commonly found on these plains in 1988–90 but were rarely found here in 1996–98. In addition, several measures of space utilization were observed to change significantly between periods (Fig. 4), and these suggested major shifts in the energetics of space utilization among Talek females. Specifically, on average in 1996–98, Talek females were found significantly farther from the communal den ($T = 4.701$, d.f. = 24, $P < 0.001$), but closer to the nearest territory boundary than in 1988–90 ($T = 6.980$, d.f. = 24, $P < 0.001$). In addition, Talek females had significantly larger home ranges in 1996–98 than in 1988–90, as reflected in mean UD size

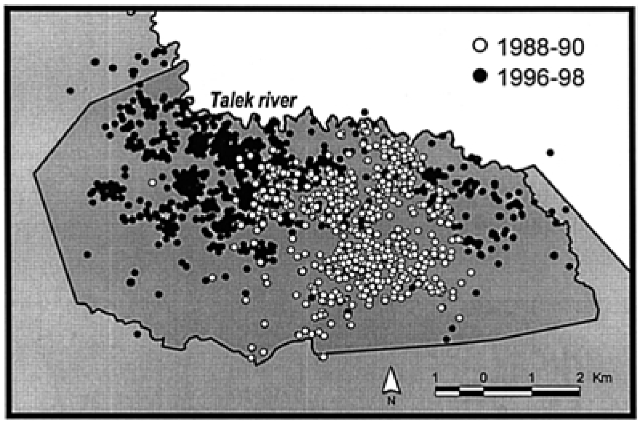

Fig. 3 Locations at which Talek females were found in 1988–90 (open circles) and 1996–98 (filled circles). Thirteen females, matched for social rank, were monitored during each 20-month period.

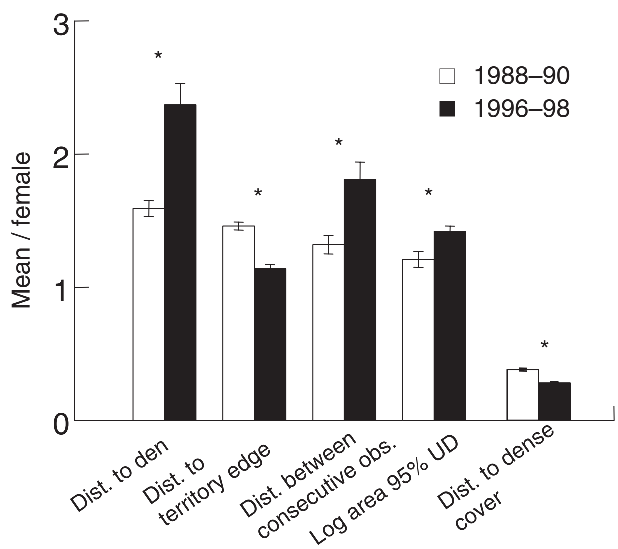

Fig. 4 Differences observed between 1988–90 and 1996–98 with respect to measures of space utilization for 13 females monitored during each time period. Asterisks indicate significant differences between means. All distances are in km. Log 95% UD values represent sizes of individual home ranges. Distance to dense cover was calculated as the linear distance between a female's location and the nearest grid cell containing dense vegetative cover.

based only on non-tracked data. In 1988–90, the mean size of the 95% UD per female was 17.7 ± 5.7 km^2, whereas it was 28.4 ± 6.3 km^2 in 1996–98 (*T*-test on log 95% UDs: $T = 3.482$, d.f. = 24, $P = 0.003$). Thus actual mean home-range size for Talek females increased by approximately 60%. This increase was not due to a greater number of observations in 1996–98 than in 1988–90; 95% UDs generated from half the 1996–98 observations were 26.9 km^2 and 29.6 km^2. Finally, mean distances between consecutive sightings for each female were significantly larger in 1996–98 than in 1988–90 ($T = 3.500$, d.f. = 24, $P < 0.005$), even though mean time between sightings was shorter in 1996–98 than in 1988–90 ($T = 2.306$, d.f. = 24, $P < 0.05$). All these indicators suggest female hyenas were expending more energy moving around their habitat in 1996–98 than in 1988–90.

Group size

On average in 1988–90, the mean number of hyenas present in 4036 observation sessions was 5.3 ± 0.1. By contrast, in 7495 sessions in 1996–98, the mean number of hyenas present was 3.3 ± 0.1. Thus mean group size decreased by 38% between periods ($T = 22.20$; d.f. = 11,529; $P < 0.001$).

Activity rhythms

The number of Talek hyenas present per session decreased significantly between 1988–89 and 1996–97 during both of our prime crepuscular observation periods (Fig. 5; morning: $T = 7.810$, d.f. = 2724, $P < 0.001$; evening: $T = 9.800$, d.f. = 1885, $P < 0.001$). Size of the Talek clan was actually larger in 1996–98 than in 1988–90 (see Table 1), so this decline could not be explained simply by the presence in the territory of fewer hyenas. Since Talek hyenas were as seldom found in the open during the midday heat in 1996–98 as they were in 1988–90, we inferred that crepuscular activity by Talek hyenas had largely been replaced by nocturnal activity between 1988–90 and 1996–98. This inference was also supported by our finding that the mean time of morning at which Talek animals were last seen tended to be earlier in 1996–98 than in 1988–90, and the first sightings of hyenas in late afternoon tended to occur later in 1996–98 than in 1988–90. Having observed changes between 1988–90 and 1996–98 with respect to the use by Talek hyenas of both space and time, we next sought correlated changes in ecological variables in order to identify possible causal agents responsible for these behavioural changes.

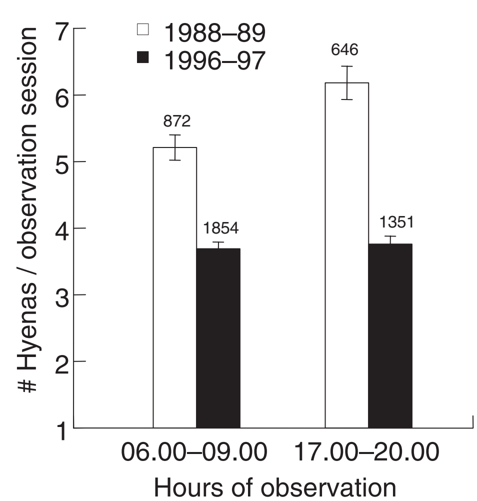

Fig. 5 Comparison between 1988–90 and 1996–98 with respect to the mean number of Talek hyenas present per observation session during crepuscular observation hours. Numbers over bars indicate total number of sessions.

Climate

In 1988–90, the Talek territory received rain on 10.6 ± 1.2 days each month, yielding a mean total of 90.4 ± 17.4 mm of rain per month. In 1996–98, the territory received rain on 11.8 ± 1.2 days each month, yielding a mean total of 118.4 ± 20.6 mm of rain per month. Neither the mean number of rainy days per month (T = –0.770, d.f. = 38, P = 0.444) nor the mean total rainfall per month (T = –1.034, d.f. = 38, P = 0.304) differed significantly between study periods. Mean monthly temperatures recorded in Nairobi increased by 0.9°C between 1988–90 and 1996–98, from 18.9 to 19.8°C. Assuming temperatures in Talek vary over time as they do in Nairobi, this suggests Talek hyenas experienced significantly higher temperatures in 1996–98 than in 1988–90 (T = –2.28, d.f. = 35, P = 0.029).

Vegetation

Although we did not have a second set of aerial photographs with which to document temporal change in vegetative cover in the Talek area, work by other investigators suggests that dense vegetative cover has declined in the Reserve over the last two decades (e.g. Homewood *et al.*, 2001; Serneels, Said & Lambin, 2001). Nevertheless, mean distances at which Talek females were found from dense vegetative cover decreased between 1988–90 and 1996–98 from 378 ± 14 m to 280 ± 17 m (Fig. 4; T = 4.5, d.f. = 24, P < 0.001). Furthermore, about a third of female locations in 1988–90 fell within 200 m of dense cover, but in 1996–98 almost half of all non-tracked locations fell within 200 m of dense cover (T = 3.50, d.f. = 24, P < 0.005). Finally, the amount of moderate or dense cover situated inside the home range used by Talek females increased from 10% to 17% as the size and shape of the collective UD changed between the time periods. Thus, Talek hyenas in 1996–98 appeared to be using bushier areas, and avoiding open areas, more than they did in 1988–90.

Lions

Lions were present in the Talek area in 1988–90 (Ogutu & Dublin, 1998). Numbers of lions were most likely either unchanged between 1988–90 and 1996–98, or lower in 1996–98 because of a severe canine distemper outbreak in 1994 that reduced lion numbers by 20–30% throughout the Serengeti-Mara ecosystem (Kock *et al.*, 2000; Packer *et al.*, 2000). Here we compared mean monthly rates at which Talek hyenas encountered lions during the two study periods, and found that these rates decreased non-significantly from 1.40% of sessions in 1988–90 to 1.03% in 1996–98 (T = 0.989, d.f. = 40, P = 0.329). Therefore it does not appear that changing rates of lion–hyena interactions could be responsible for the changes we observed between periods in patterns of hyena space utilization.

Ungulate prey

Numbers of ungulates counted on short-grass and long-grass transects (shown in Fig. 1(b)) were similar between 1988–90 and 1996–98 with respect to both abundance and seasonal patterns in the two habitat types (Fig. 6). On average during both periods, prey were three to six times more abundant on short-grass plains than on long-grass plains. Mean prey abundance estimated bi-weekly on the short-grass transect did not differ significantly between 1988–90 and 1996–98 (246 ± 14 ungulates in 1988–90 versus 293 ± 26 ungulates in 1996–96; T = –1.159, d.f. = 71, P = 0.246). However, means increased significantly between periods for the long-grass transect (44 ± 14 ungulates in 1988–90 versus 112 ± 24 ungulates in 1996–96; T = –2.313, d.f. = 71, P = 0.024).

Tourism

Although numbers of hotels and beds available in the Reserve increased between 1988–90 and 1996–98 (Bhandari, 1999), fewer tourists were recorded entering the Reserve in 1996–98 than in 1988–90. On average, 177,574 ± 16,140 tourists were recorded entering the Reserve per year in 1989–90 (Gakahu, 1992) while in 1997–98, annual tourist numbers averaged below 100,000 per year (Walpole *et al.*, 2003).

Settlements and livestock

Numbers of pastoralist settlements along the edge of the Reserve, and use of Reserve land for grazing, increased between 1988–90 and 1996–98. Numbers of settlements doubled along the Talek river north and east of the Talek

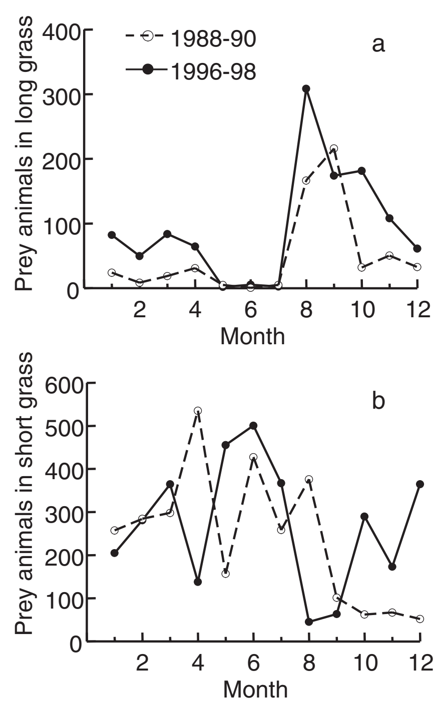

Fig. 6 Monthly averages of bi-weekly prey counts for (a) the long-grass and (b) the short-grass transects indicated in Fig. 1(b). Most months include data from 2 years, but April–August include data from only 1 year.

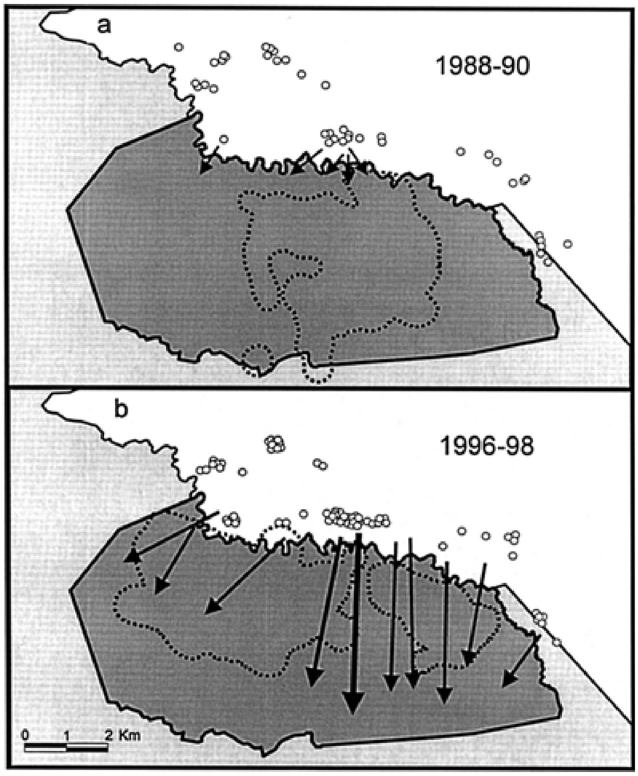

Fig. 7 Locations of pastoralist villages and corrals (empty circles) shown in relation to the collective 95% UD contours generated by spatial locations obtained for 13 Talek females in (a) 1988–90 and (b) 1996–98. Arrows show daily travel routes for cattle herds, and arrow width indicates relative numbers of cattle travelling these routes.

clan territory between 1991 (n = 36; Fig. 7(a)) and 2000 (n = 72; Fig. 7(b)). Settlements were also more highly concentrated near the Reserve boundary in 2000 than in 1991, increasing from 11 in 1991 that were within 1 km of the Talek river (Fig. 7(a)) to 39 in 2000 (Fig. 7(b)). It is worth noting that livestock observed in the Talek clan's territory in 1988–90 occurred in tiny herds that tended to remain very close to the Talek river (Holekamp & Smale, 1992). At most, grazing in the Reserve in 1988–90 occurred on 30–35% of observation days (Holekamp & Smale, 1992), compared to grazing on 90% of days in 1996–98.

Demography

All but two of our demographic measures differed significantly between 1988–90 and 1996–98 (Table 1). Clan size, number of adults, number of adult females, adult sex ratio and juvenile mortality increased, while number of juveniles decreased. Adult female mortality and birth rate did not change significantly between the two time periods.

DISCUSSION

Ecological correlates of hyena space utilization patterns in 1996–98

We expected that Talek hyenas would utilize space in a fashion permitting them to maximize foraging efficiency while minimizing risk of injury and death. However our results suggest that minimizing risk strongly affected patterns of space utilization in 1996–98, and that this may have occurred at some cost to foraging efficiency. That is, since prey was unevenly distributed within the Talek territory, we expected that hyenas would forage in areas of highest prey density to minimize search time and maximize encounter rates with prey. Instead we found that, although hyenas were unlikely to be found in areas of lowest prey abundance in 1996–98, they were equally unlikely to be found in the grid cells containing most prey. The short-grass plain containing the highest herbivore density was centrally located and held almost a quarter of the total prey available within the Talek territory at any given time. This prey-rich area should have been an attractive foraging site for Talek hyenas, yet they rarely even passed through it. Instead hyenas were often found to the east and west of it, and their movement patterns suggested that they were actively avoiding this site by travelling around it when crossing their territory. In earlier studies of *Crocuta* in this Reserve and other protected areas across the African continent, both locations at which hyenas occur, and their movements within their home ranges, are strongly and positively correlated with local prey abundance (Kruuk, 1972; Skinner & van Aarde, 1980; Tilson & Hamilton, 1984; Frank, 1986*a*; Cooper, 1990*b*; Mills, 1990; Gasaway, Mossestad & Stander, 1991; Hofer & East, 1993*a*,*b*,*c*; Hofer, East & Campbell, 1993). Thus the tendency of Talek hyenas in the late 1990s to avoid the area within their territory that contained most prey appears to be entirely unique.

Table 1 Comparison of demographic measures between 1988–90 and 1996–98.

Variable	1988–90[a]	1996–98[a]	U^{b}	P^{c}	Percent change[d]
Clan size	65.8 + 1.2	72.7 + 2.0	100.00	<0.05	10.41
%Adults	42.8 + 1.2	50.9 + 1.1	48.00	<0.05	18.93
%AFem	28.6 + 0.7	31.1 + 0.6	101.00	<0.05	8.41
%Juv	45.2 + 0.02	33.3 + 0.01	367.00	<0.05	–26.33
Sex ratio	0.49 + 0.02	0.64 + 0.02	42.00	<0.05	29.21
AFem mortality	0.024 + 0.009	0.014 + 0.005	217.00	NS	–41.67
Juv mortality	0.027 + 0.007	0.072 + 0.013	116.50	<0.05	166.67
Birth rate	0.10 + 0.03	0.11 + 0.03	190.50	NS	10.68

[a]Mean (±SE).
[b]Mann–Whitney U-test, n_1 = 20 and n_2 = 20 for all tests.
[c]All P-values are corrected for multiple tests using a sequential Bonferroni adjustment.
[d]Positive values indicate an increase over time; negative values indicate a decrease over time.

The two main sources of mortality for spotted hyenas are lions and people (Kruuk, 1972; Hofer *et al.*, 1993). We expected that Talek hyenas might therefore occupy spaces that were not likely to be occupied by lions or humans. In contrast to our expectation in regard to lions, we found that hyenas frequently used the same grid cells as lions, and that the spatial distributions of the two species were positively correlated. Thus the spatial overlap between these two competing species documented at coarse spatial scales (e.g. Mills & Gorman, 1997) appears to occur at finer spatial scales as well. However, Talek hyenas did appear to avoid areas of heavy human use within the Reserve.

Two forms of anthropogenic activity may account for the odd distribution of locations at which we found Talek hyenas in 1996–98: tourism and pastoralism. Our data did not support predictions of the tourism hypothesis. Hyenas tended to be found closer to dens when greater numbers of tour vehicles were present, and there was no difference based on numbers of vehicles with respect to distances at which hyenas were found from the edge of the territory.

Large numbers of cattle grazed inside the Talek territory on 90% of observation days in 1996–98. As cattle moved in and out of the Reserve across the Talek river, the area south of the river was generally heavily utilized either for grazing or for herd transit to other areas. The central short-grass plain on which wild herbivore density was highest was also the area of the Talek territory in which livestock grazing was heaviest. Even though most of the territory defended by the Talek clan was comprised of open grassland, female hyenas were found disproportionately often in close proximity to dense vegetative cover. Clearly hyenas did utilize some areas grazed by cattle in 1996–98, but the areas that hyenas shared with livestock tended to contain denser vegetation offering protective cover from the herders who guarded cattle. Indeed, herders sometimes harassed or killed hyenas when they encountered them (K. E. Holekamp, unpubl. data).

Historical comparison

Use by Talek hyenas of both space and time, as well as their average group sizes, changed significantly in less than a decade, and these behavioural changes were also associated with demographic changes. In 1996–98, Talek females were found closer to territory boundaries, farther from dens and closer to dense vegetative cover than in 1988–90. Talek females also travelled greater distances between consecutive sightings in 1996–98, and they occupied significantly larger home ranges, as described by their 95% UDs. Between 1988–90 and 1996–98, group size decreased by 55%, indicating that, in addition to movements and activity, social behaviour was affected here by changes in prevailing ecological conditions.

Between 1988–90 and 1996–98, hyenas also significantly reduced their crepuscular activity. Since Talek hyenas were rarely found active between 09.00 and 17.00 hours in either 1988–90 or 1996–98, we infer that they became much more nocturnal between these two periods. Although 24-hour follows would be required to document precisely how activity patterns have changed among Talek hyenas, our current data strongly suggest that their circadian activity rhythms have shifted considerably during the past decade.

Spotted hyenas inhabiting very hot, dry habitats are almost exclusively nocturnal in their daily activity (Tilson & Hamilton, 1984; Cooper, 1990*a*; Mills, 1990). However, elsewhere in Africa, where daytime temperatures are lower, *Crocuta* are commonly active during daylight hours (e.g. Kruuk, 1972; Frank, 1986*b*). Nevertheless, even hyenas living in mild climates tend to become extremely nocturnal, and prefer habitat with heavy vegetative cover, in areas characterized by intensive livestock grazing (Frank & Woodroffe, 2001). Similarly, *Crocuta* become exceptionally shy of human activity in areas where they are poached (e.g. Korb, 2000). We suggest that the changes observed in temporal activity patterning among our study animals between 1988–90 and 1996–98 may represent a comparable response to increasing diurnal pastoralist activity inside the Talek territory. Similar shifts in activity rhythms have also been documented in other carnivore species in association with altered levels of human activity in other parts of the world (e.g. Kitchen, Gese & Schauster, 2000).

Changes in use of space and time were associated with demographic change among Talek hyenas. Interestingly, adult female mortality actually decreased between 1988–90 and 1996–98, and overall clan size increased by approximately 8%. This increase in clan size was associated with a 9% increase in the size of the defended Talek territory that occurred in 1995, which appeared to be due to a shift in the territorial boundaries of one adjacent clan. In any case, hyena density within the Talek territory did not change appreciably between 1988–90 and 1996–98, even though clan size increased. The largest demographic change was the 2.7-fold increase in juvenile mortality rate. Less than 15% of the overall juvenile mortality with known sources in 1996–98 was due to human activity, but our sample of cases in which cause of death was known was very small. We therefore emphasize here that interpretation of our demographic data is rendered difficult by the fact that we compared measures calculated for only two 20-month intervals. At this point, the demographic changes we observed between periods suggest only that we should continue closely monitoring the Talek area in future to ascertain whether long-term changes are taking place in the structure of this ecological community.

It seems unlikely that meteorological differences between 1988–90 and 1996–98 can account for the behavioural and demographic changes we observed. Rainfall did not differ significantly between the two periods, and although increased temperature might promote more nocturnal activity, it cannot easily explain altered demography, social behaviour or patterns of space utilization. Similarly, rates of lion–hyena interaction did not change between periods, so these cannot explain the differences we observed. Our data documenting rates of encounters between lions and hyenas do not directly address the question of whether changes occurred between periods in risks associated with interspecific competition or intraguild predation. However, since lion population density was known not to increase between periods, altered levels of risk from lions cannot explain the behavioural or demographic changes observed here. The abundance of wild ungulates increased significantly between 1988–90 and 1996–98 on tall-grass plains, but no change was observed on short-grass plains. Thus the failure of Talek hyenas to utilize the latter in 1996–98 cannot be explained by reduced prey abundance there.

Throughout both study periods, tourist vehicles were commonly in the Reserve from 07.00 to 09.00, and again from 16.30 to 18.30 hours. Although these visitation hours overlapped with daily periods of peak hyena activity in 1988–90, our data failed to support a hypothesis suggesting that increasing levels of tourist visitation might be responsible for the changes we observed in hyenas' use of either space or time. The circadian patterns of tourist visitation did not change between 1988–90 and 1996–98, yet hyena activity patterns became significantly more nocturnal. Although we did not record tourist numbers or impacts in the Talek area in both study periods, numbers of tourists recorded entering the Reserve appear to have declined. Thus it does not seem likely that changes in tourism can account for changes in hyena behaviour or demography.

The most striking change in the Talek ecosystem documented between 1988–90 and 1996–98 was the increase in human population density along the Reserve boundary, and the increased reliance on Reserve land for livestock grazing. In 1996–98, but not in 1988–90, cattle grazed heavily in the interior of the Talek clan's territory. Although we did not attempt to record livestock and hyena locations simultaneously, we did see hyenas being displaced by cattle from resting and feeding sites, and we observed hyenas emerging from bushes soon after livestock herds had passed through an area. That hyenas avoided the centre of their territory in 1996–98 even when no cattle were present may be a indication that encounters with herders had increased over time and that the daily window of time in which hyenas could utilize the short-grass area undisturbed had become quite small.

Our results indicate that Talek hyenas altered their use of both space and time in order to avoid pastoralists. The behavioural and demographic changes documented here among Talek hyenas can thus best be explained by increased grazing activity and erosion of the Reserve boundary. Even though both harassment of wildlife and regular livestock grazing are forbidden within the Reserve (Kenyan Wildlife Act, 1989), these regulations are rarely enforced (Walpole *et al*., 2003). That Talek hyenas altered their use of space and time within a period of only a few years indicates that these animals can respond very rapidly to changing ecological conditions. If indeed increased pastoralist activity within the Talek area has effected the behavioural changes described here, we expect initiation of enforcement of park regulations would cause use of space and time by Talek hyenas to return to patterns like those observed in the late 1980s.

The striking plasticity characteristic of spotted hyenas is clearly reflected in our data documenting their ranging behaviour, habitat preferences, group size and temporal patterning of activity. We suspect this behavioural plasticity may help *Crocuta* survive in the face of burgeoning anthropogenic activity even when less flexible carnivore species show pronounced population declines (Gittleman *et al*., 2001). Other large mammals in the Reserve are clearly declining, and livestock grazing has been identified as one causal factor responsible for such declines (e.g. Ottichilo, De Leeuw & Prins, 2001). Density of spotted hyenas has not declined, yet their behavioural changes described here may represent warning signs of serious environmental degradation in this important ecosystem.

Acknowledgements

We thank the Office of the President of Kenya for permission to conduct this research. All work reported here was conducted in accordance with Kenyan law. We thank the Kenya Wildlife Service, the Narok County Council, and the Senior Warden of the Masai Mara National Reserve for their cooperation. We thank N. E. Berry, S. M. Cooper, S. M. Dloniak, M. Durham, A. L. Engh, J. Friedman, P. Garrett, I. Graham, K. Greene, T. H. Harty, C. I. Katona, K. Nutt, G. Ording, L. Smale, S. A. Wahaj, K. Weibel and B. White for their assistance in the field. We thank M. Walpole for help in tracking down data on tourism and climate, and P. Bills for help with data extraction. We thank C. Barber, G. Bradshaw, W. Chomentowski, J. Kolowski, D. Skole and S. Smith for their help with extraction, entry and analysis of spatial data. This work was supported by NSF grants BNS8706939, BNS9021461, IBN9309805, IBN9630667 IBN9906445 and IBN0113170.

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